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LARGE PLEISTOCENE FELINES OF NORTH AMERICA

BY GEORGE GAYLORD SIMPSON

About thirty occurrences of true cats, felines, of the size of pumas or larger have been reported in the Pleistocene of North America. Except for the specimens from the asphalt of Rancho La Brea and of McKittrick, in California, these are nevertheless relatively rare fossils and the specimens are usually fragmentary. They have been assigned by various students to about fifteen different species and their affinities and taxonomy have not been understood. Many have been placed in extinct, or supposedly extinct, species with no definite idea as to their relationships to other cats. A few have been recognized as pumas, or as related to pumas, but on the other hand some that are pumas beyond much doubt have been sharply separated from that group. Others have loosely been called "lions" or "tigers" without clear demonstration of a reason for such explicit terms and in spite of the fact that they are related only remotely and not in any exclusive way to those Old World forms. There has indeed been a general tendency to compare our larger fossil felines with those of the Eastern Hemisphere and to minimize or omit entirely comparisons with other American cats, in spite of the fact that the latter comparisons would seem more obvious and are in most cases, perhaps in all, truer indications of affinity. It is particularly striking that (with one cryptic and unexplained partial exception, noted later) no one seems to have reported jaguars in the Pleistocene of the United States and few have seriously considered this rather obvious possibility.

It is the purpose of the present paper to make a summary review of these discoveries and to attempt to establish some order in this confusion. As usual, many problems remain unsolved and not all loose ends can be gathered, but on present evidence it seems possible to establish the following conclusions:

1.—Known large Pleistocene felines from North America suffice to demonstrate the presence of three, and only three, groups: pumas, jaguars, and *P. atrox*.

2.—Although scattered from the Atlantic to the Pacific Coasts, the Pleistocene pumas do not, in the known parts, show much if any more variation than do recent pumas of one subspecies and of more limited geographic distribution. They average a little larger than recent pumas and show minor morphologic distinction of not more than specific value and possibly less. The definitions of the several supposedly distinct groups are not yet satisfactory.

3.—True jaguars specifically inseparable from *Panthera onca*, the living species, occur widely. They may (doubtfully) average somewhat larger than the largest living races and may be tentatively distinguished as *P. onca augusta*. No local differences within North America are demonstrated by the known materials.

4.—*Panthera atrox*, the so-called American lion, is not a lion and might be called a giant jaguar, clearly distinct specifically from *P. onca* but nevertheless related to it.

The evidence for these views will be briefly summarized in this paper.

As acknowledged in more detail elsewhere,[1] I am much indebted to Dr. W. J. Cameron and Mr. W. E. Michael for the specimens of fossil jaguars from Tennessee described in this paper. I am also indebted to Dr. C. L. Gazin for the opportunity to study several types and other specimens in the collection of the U. S. National Museum, for the loan of an important, undescribed specimen collected by J. W. Gidley in Florida, and for permission to describe and figure this specimen here. The Department of Mammalogy of this Museum has provided a large number of recent specimens for comparison. Dr. Anne Roe

[1] Amer. Mus. Novitates, No. 1131.

Simpson has read the manuscript and offered useful suggestions on several points.

The drawings in this paper were made by J. C. Germann.

NORTH AMERICAN FOSSIL JAGUARS

The certain identification and determination of the affinities of the large cats demand associated dentitions, at least, since even forms as dissimilar as jaguars and pumas are much alike as regards isolated teeth or many skeletal fragments. It is probable that specimens described as long ago as 1872 and at intervals since then are, in fact, jaguars, but only now is it possible to prove that these animals did live in North America, well outside their present range, during the Pleistocene. Various American fossils have been compared with jaguars, as well as with lions, tigers, and other forms in reality more distantly related, but a positive identification is now made possible for the first time by three relatively good specimens, Amer. Mus. Nos. 32633 and 32635 and U.S. Nat. Mus. No. 11470.

These American Museum specimens were found in Craighead Caverns, near Sweetwater, Tennessee. An account of their discovery and peculiar occurrence is being given elsewhere and need not be repeated here.[1] Amer. Mus. No. 32633 (Fig. 1) includes the right ramus of the lower jaw, lacking the incisors, which had dropped out after death, and the coronoid process and medial portion of the articular condyle, gnawed off by rodents. The symphysial portion of the left ramus, with the canine but without the incisors was also found. The symphysis was open and the two sides separated, although they certainly belong to one individual. Posterior to the canine the left ramus had been broken and the surface is gnawed. There is a slight rim of calcareous material near this break and it has been suggested that this represents healing of a jaw fractured during life, but I think it more probably postmortem and representative of contact with the surface of the dirt, the protruding part having been gnawed away. The cheek teeth show considerable wear but the cusp arrangement is still well visible. The right canine had apparently been broken off during life and the stump later much worn by use—this is a common occurrence among recent jaguars. The left canine had not been broken, unless possibly at the tip, but is also much worn, especially on the posterior side.

This jaw considerably resembles *Panthera atrox*, indeed it probably has no morphological characters that do not occur as variations in that species, which is very jaguar-like in this part and most others. It is, however, significantly smaller than any of the fine series of *P. atrox* jaws now known, even if the relatively small "*Felis imperialis*" be included in *P. atrox* as Merriam and Stock suggest and as I also think proper.

In every character, including size and proportions, the fossil jaw closely approaches the largest living jaguars. Comparisons were made especially with a series of eight recent specimens of *Panthera onca milleri*, which is among the largest, but is not the largest, of recent groups. All strictly morphological features of the fossil can be almost exactly matched in this subspecies. The fossil jaw is slightly deeper (not longer), but not significantly more deep in a statistical sense, than in large males of the recent group. The canine is unusually stout, but again the difference is slight and not significant. The cheek teeth are not significantly wider, but are significantly longer both absolutely and relatively, although the difference from the largest *milleri* males is not great. They compare as follows:

	P. onca milleri (N = 8)		d of Amer. Mus. No. 32633 from *milleri*	
Variate	Mean	σ'	mean	d/σ'
LP_3	15.19	.99	3.01	3.0
LP_4	21.26	.86	3.44	4.0
LM_1	21.16	1.25	3.44	2.8

[1] Amer. Mus. Novitates, No. 1131.

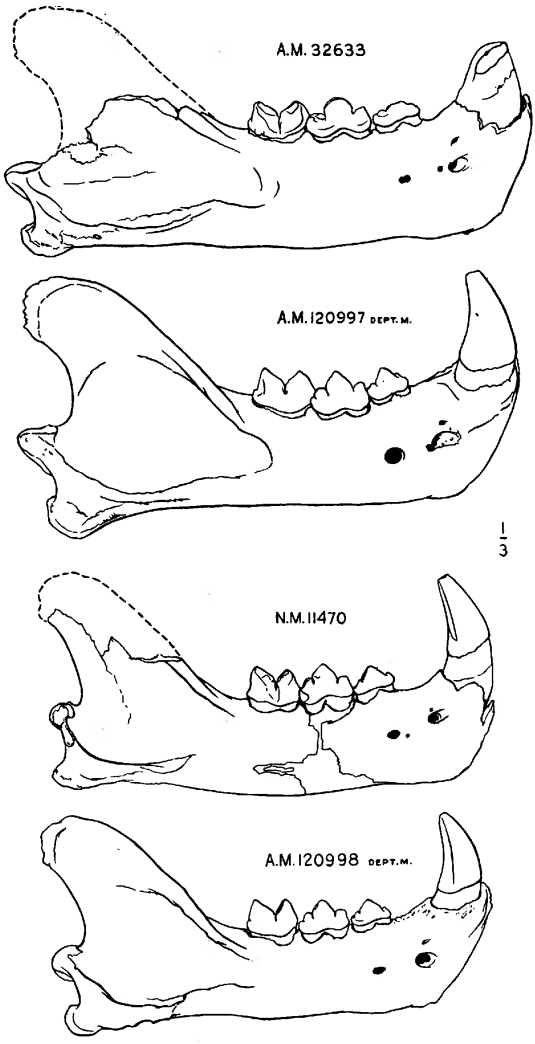

Fig. 1. Lower jaws of fossil and recent jaguars. A.M. No. 32633, *Panthera onca augusta*, presumed male, subfossil, Craighead Caverns, Tennessee. A.M. No. 120997 (Dept. Mammalogy), *Panthera onca milleri*, male, recent, Matto Grosso. N. M. 11470, *Panthera onca augusta*, presumed female, fossil, Melbourne Formation, Melbourne, Florida. A.M. No. 120998 (Dept. Mammalogy), *Panthera onca milleri*, female, recent, Matto Grosso. All one-third natural size.

I do not have an adequate series of the largest living subspecies, *P. o. palustris*, but the lengths of these teeth in the Tennessee fossil are probably within the range for that subspecies, surely so as regards M_1 for which Cabrera (1934) has given ten measurements. For this series M = 22.80, σ' = 1.18, d for the Tennessee specimen = 1.8, and d/σ' = 1.5, far from significant. On the available data I do not, indeed, find any way to distinguish this fossil from the large living males of *P. o. palustris*.[1]

Amer. Mus. No. 32635 (Fig. 2) was also found in Craighead Caverns and in the same fissure as the jaw just discussed, although some distance from it and higher in elevation. The teeth are less worn and cluding their palatal processes, and the anterior part of the jugal and a fragment of the right nasal are also preserved. Near this and apparently belonging to the same individual were found the nearly complete zygomatic process and a small part of the articular process of the left squamosal and another piece with much of the right ear region, including the inner half of the glenoid fossa, post-glenoid and post-tympanic processes, adjacent parts of the squamosal, outer and anterior parts of the tympanic, and the complete petrosal.

Like Amer. Mus. No. 32633, these parts agree very closely with recent jaguars and are in all respects near or within the known range of variation of large males of *P. onca*

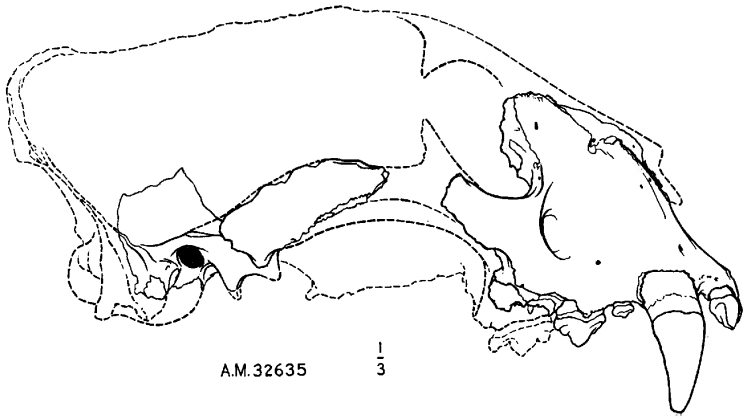

Fig. 2. *Panthera onca augusta*, restoration of right lateral view of skull, probably male. Parts in continuous lines are Amer. Mus. No. 32635, from Craighead Caverns, Tennessee. Zygomatic fragment is reversed from the left side. Parts in broken lines restored with reference to recent *Felis onca* skulls. One-third natural size.

do not occlude well, so that this specimen probably represents a second individual. The right side of the face is represented, with I^{1-3}, C, and P^{2-3}. The premaxilla and maxilla are practically complete, in-

palustris or *P. o. milleri*. In the upper dentition (unfortunately lacking the characteristic carnassial) the only definite distinction from our *P. o. milleri* series is the greater length of P^2, 8.5 mm. as opposed to 7.28 mean and 7.7 maximum observed

[1] This is the subspecies usually called *Panthera onca paraguensis*. On the nomenclature of this group see Cabrera, 1934. Incidentally Cabrera notes that the whereabouts of the type of *Felis onca antiqua* Ameghino, 1889, is unknown to him and he discusses this form on the basis of a cast. The original was sold by Ameghino to Cope and by Cope to this Museum, where it is now permanently preserved as fossil mammal No. 11107. I have examined it and agree with Cabrera's conclusion that it is inseparable from *P. onca palustris*.

The subspecific separation of *P. onca milleri* from *P. o. palustris* is uncertain, although *milleri* does represent a local group, race or stirps, with slightly different average characters.

Throughout this paper all recent jaguars are considered as belonging to one species, *Panthera onca*, following Nelson and Goldman, 1933, and other good recent authorities. The living pumas are similarly all referred to *Felis concolor*. In both these cases the degree of divergence and the character of distribution is typically that of geographic races and subspecies, not of several well-defined full species according to the best usage.

Finally on the subject of nomenclature it is noted that the name *onca* should be pronounced "onsa" and not "onka," but the otherwise preferable spelling *onça* is not permissible because Linnaeus wrote *onca*.

in our recent series of eight specimens. Although small, the difference is significant ($d/\sigma' = 3.7$) and the race represented by the fossil did have a larger P^2 than does this recent race, both absolutely and relative to the width of the same tooth. It may not have differed significantly from *P. o. palustris* which has on an average a larger dentition than *milleri* and for which I do not have an adequate series of measurements of P^2. There are no other apparently significant differences in size or structure of the dentition.

The osteology of the preserved parts of the face appears to be within the range of either of the recent subspecies mentioned and, except for size, of recent jaguars generally. An interesting feature is the presence of a shallow, irregular pit on the maxillo-nasal suture immediately posterior to the ascending process of the premaxilla. This apparently represents a puncture, such as would be made by the canine of another jaguar, healed during life. Such scars are very common among recent jaguars, usually on males, to such an extent that they could almost be considered as secondary (or tertiary) sexual characters. All of our wild-collected and definitely sexed male *milleri* skulls have such head scars, in one case (Dept. Mam. No. 36950) in almost the same position as in the fossil. None of the definitely sexed or probable females has similar scars. Although obviously inconclusive, this is serious evidence that the fossil is a male, a matter of some taxonomic importance as will appear.

The zygomatic process of the squamosal is not very characteristic and requires no more comment than to say that it is almost exactly like the same part in large recent jaguars. The rugosities on the temporal surface of the root are a little more prominent than in my comparative specimens, but this has no apparent significance.

The auditory region, on the other hand, has great value in determining affinities despite the fact that it shows a surprising amount of variation. For instance, the degree of application of the mastoid process to the bulla gives rise to striking differences. The two are sometimes smoothly continuous and sometimes separated by a groove which may be deep or shallow, broadly rounded or narrow and fissure-like. But all these variations may occur (among jaguars, at least) not only in one subspecies but also in one interbreeding local stock. Indeed in one of the female *milleri* specimens this character is markedly different on the two sides of the same skull. (The fossil has a broad groove with rounded bottom and of moderate depth.)

Here again this part is basically jaguar-like throughout in the Craighead cat. The distance from the post-glenoid process to the posterior part of the mastoid process is shorter and the lateral exposure of the mastoid process is smaller than in recent comparative specimens of similar size, but the difference is so slight and the variation so great that this observation has no necessary significance. Another unusual but not unique feature of doubtful significance is the clarity and size of a pit (foramen spinosum?) anterior to the external auditory meatus and immediately medial to the post-glenoid process, and the development from the tympanic of a prominent spine medial to this.

Found near these skull parts was the articular end of a right scapula, Amer. Mus. No. 32638, and a left second metatarsal, Amer. Mus. No. 32637. These also belong to a jaguar and probably to one of the individuals represented by the jaw and skull parts (or possibly, but improbably, all are of one individual), but association is not demonstrated. The scapula has been much gnawed by rodents. As far as can be judged by what remains, which is characteristic enough for fair identification, it closely resembled the same part in a large recent jaguar. The metatarsal is perfectly preserved and is particularly valuable because the metapodials are among the most characteristic parts of the jaguar and permit unequivocal identification at least as far as the species. This specimen is decisively like *P. onca* in all important respects. In comparison with my limited recent material, the mesocuneiform articular surface extends farther on the head in a plantar direction, the process that abuts against the first metatarsal is more prominent and more distal, and the shaft is less

curved. These small differences in variable features are outweighted by the general agreement, especially since the available comparative specimens are from zoo animals and the slight differences do not constitute definite resemblances to other known species.

The principal measurements of this bone are as follows:

Greatest length	84.2 mm.
Dorsoventral diameter on outer face of proximal end	20.6
Greatest transverse diameter of articulation on proximal end	12.2
Least transverse diameter of shaft	11.9
Transverse diameter of distal end of shaft	16.6

like *P. atrox*, and quite different from the puma.

Taken together, the Craighead Caverns specimens include many fully identifiable features and leave no possible doubt that they do represent a jaguar inseparable from *Panthera onca*, if that species be used to include all recent jaguars as is now generally done.

This positive identification and spread of material for comparison makes possible the more tentative identification of various similar but less complete specimens found previously. Of these by far the best is US. Nat. Mus. No. 11470, collected by

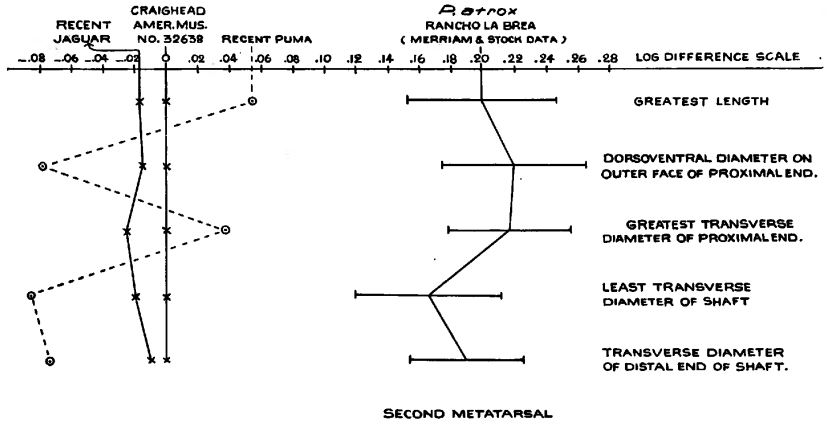

Fig. 3. Ratio diagram of dimensions of second metatarsal in various large felines, as labeled. Recent jaguar and puma, one specimen of each in American Museum. *P. atrox*, large Rancho La Brea sample, data from Merriam and Stock; horizontal lines show observed ranges. For method of construction and interpretation of this and other ratio diagrams (Figs. 6–10) see notes at end of text.

The accompanying ratio diagram, Fig. 3, compares the proportions of this bone to homologous elements in some other cats. The construction and interpretation of such diagrams are explained at the end of this paper. It is noted there that (with the arrangement used in this figure) closer approach to a single vertical of observations on a form used for comparison means closer approximation of proportions to those being compared, which are arbitrarily set in a straight vertical line. The diagram therefore shows that the proportions of the Craighead metatarsal are almost exactly as in the recent jaguar, somewhat, but less, the late Dr. J. W. Gidley at Melbourne, Fla., in 1926 but not hitherto published. It is not exactly labeled as to horizon but doubtless came from the "No. 2 bed" or Melbourne Formation, considered by Hay to belong to the first interglacial stage but by most other students believed to be late or latest Pleistocene. This specimen is included in this study through the courtesy of Dr. C. L. Gazin. In a list of Melbourne fossils prepared by Gidley and published by Hay (1927) the entry "*Felis centralis?*" appears without comment. "*Felis centralis*" is the Central American jaguar, *Panthera onca centralis*. Gidley's label

on this specimen is "*Felis* cf. *veronis* Hay," but it is probably the basis for his queried identification as *F. centralis*. Both identifications appear to me to be correct to the point of recognizing the specimen as a jaguar and placing *F. veronis* also in that group.

The specimen is a right lower jaw with the canine and P_3–M_1, the central part of the ramus somewhat broken, the incisive region and tip of the coronoid broken away and lost, and the ends of the articular condyle abraded. This animal certainly is a jaguar and is in every respect within the known range of living *Panthera onca*. It can be almost exactly matched among recent specimens. It is smaller and more lightly built throughout than the Tennessee jaw and these characters, together with the rather feeble carnassial, do make it resemble the small race *P. onca centralis* as Gidley's apparent identification implies. Nevertheless it is possible and I think probable that it belongs to the same group as the notably more massive Craighead Caverns cats. Recent jaguars, as well as the Old World species of *Panthera*, show marked sexual dimorphism, the females being smaller and more lightly built than the males. The differences between this Melbourne specimen and those from Craighead Caverns are about what would be expected if the former were a female and the latter a male. For instance, as is evident in Fig. 1, the Melbourne specimen agrees closely with rather large females of *P. onca milleri* and the Craighead Caverns specimens similarly agree with large males of the same subspecies. Moreover, as will be shown, "*Felis veronis*" is a form comparable in size with that from Craighead Caverns and this supposed species certainly lived in direct association with this Melbourne cat. These facts seem to me to admit no other reasonable interpretation than that U. S. Nat. Mus. No. 11470 is a female of "*F. veronis*."

Felis veronis Hay, 1919, was based on an isolated left P^4 from Vero, Florida, in the same bed as the Melbourne jaw but at a different locality. Since the jaguar specimens hitherto discussed do not include P^4 direct comparison is impossible. Hay compared this specimen with the (Asiatic) tiger and the jaguar and, while he did not definitely commit himself, he seems to have felt that it was closer to the tiger.[1] He said that it differed from the jaguar in the presence of a "preanterior tubercle," less reduced protocone, relatively lower main cusp, and greater size. These distinctions are all invalid. Within a single subspecies, recent jaguars may lack the "preanterior tubercle" on P^4 or may have one notably larger than in the type of *F. veronis*. The development of the protocone averages about as in *F. veronis* and may be greater or less. In the series of *P. onca milleri* skulls the relative height of the main cusp of P^4 is almost exactly as in *F. veronis*. Although Hay's type is at about the maximum known size for P^4 in recent jaguars, it is within the range of the large race *P. onca palustris*, in which the length of this tooth reaches at least 33 mm. (Cabrera), which is the length of the type of *F. veronis* (to two significant figures).

It is difficult and occasionally impossible to distinguish recent feline species from isolated P^4 alone, so that demonstration that there is no definite distinction between this tooth in *F. veronis* and in *P. onca* does not absolutely demonstrate an identity. It is, however, very suggestive. *F. veronis* is significantly smaller than *P. atrox* and significantly larger than any known fossil or recent pumas. Such North American specimens as are of comparable size and more definitely identifiable now prove to belong to *P. onca*. Moreover *P. onca* is now shown to occur at the same horizon as the type of *F. veronis* and at a nearby locality. All these considerations make it as nearly certain as may be without the discovery of more complete upper dentitions that *F. veronis* is a jaguar doubtfully or not separable from *Panthera onca*.

The animal to which the type of *F. veronis* belonged was of about the size of the large lower jaw from Craighead Caverns. In eight specimens of *P. onca milleri* the ratio length M_1 : length P^4 ranges from .74 to .79, mean .755. M_1 in the Craighead cat is 24.6 mm. in length, so that its P^4 was about

[1] In subsequent non-technical accounts he called it a tiger, without other specification.

33 mm. in length, with a possible range of about 31 to 33½. P^4 of *F. veronis* is 33 mm. long, and hence suited to be the upper carnassial of an animal of the size of the Craighead cat as is also evident in Fig. 4.

F. augustus Leidy, 1872, was based on a small fragment of upper jaw with P^4 and

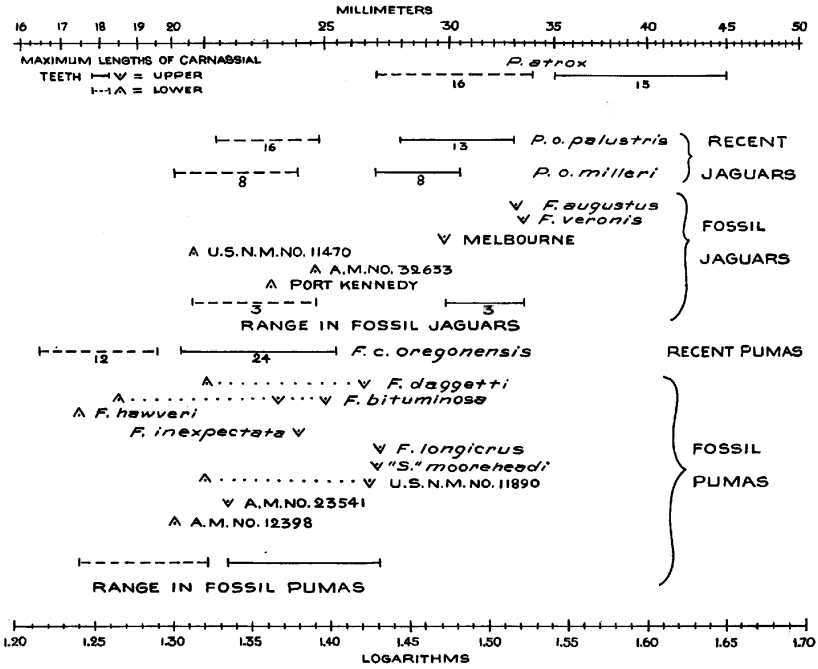

Fig. 4. Logarithmic plot of absolute lengths (not ratios) of upper and lower carnassials in various large felines, as labeled. Dots in carets represent single specimens, horizontal lines groups of specimens, their number given below the line. *P. atrox*, sample from Rancho La Brea, data from Merriam and Stock. *P. o. milleri*, living in Matto Grosso, American Museum specimens. *F. augustus*, type. *F. veronis*, type. Melbourne, unnumbered specimen from that locality in U.S. Nat. Mus. U.S.N.M. No. 11470, also from Melbourne. A.M. No. 32633, the Craighead Cat. Port Kennedy, specimen from the locality referred to *F. inexpectata* by Cope. *F. c. oregonensis*, living in northwestern U. S., includes some specimens referred to *F. c. hippolestes*, data from C. H. Merriam and from J. C. Merriam and C. Stock. *F. daggetti*, type and referred, data from Merriam and Stock. *F. bituminosa*, type and referred, data from Merriam and Stock. *F. hawveri*, type, data from Stock. *F. inexpectata*, type, data from Cope. *F. longicrus*, type. *"S." mooreheadi*, type. U.S.N.M. No. 11890, from Cumberland Cave, data from Gidley and Gazin. A.M. No. 23541, from Seminole Field, Florida. A.M. No. 23541, from Conard Fissure, referred to *"F. cougar"* by Brown.

(Logarithmic plotting is used because it represents equal relative variation by equal horizontal distances.)

the middle and posterior parts of P^3, collected by F. B. Hayden on the Niobrara River, Nebraska. It was described as from the "Loup Fork" and as of Miocene age. This age assignment appears to have gone unchallenged ever since and has prevented the careful comparison of the specimen with the large Pleistocene felines. The occurrence in the Miocene of a species of the recent genus *Felis*, even *sensu latissimo*, is evidently anomalous but has not been the subject of very explicit comment. It was perhaps on this basis, and certainly not from examination of the specimen, that Matthew (e.g., 1909, p. 116) referred the species questionably to *"Machaerodus,"* a genus to which it cannot possibly belong.

The apparent explanation of the anomaly is that the age assignment, not the generic assignment (*sensu lato*), is wrong. Leidy's "Loup Fork" materials included specimens from several quite distinct horizons, ranging from Miocene to Pleistocene

in age. The present specimen can be referred to the Pleistocene with little question, on this evidence:

a.—Some unquestionably Pleistocene specimens were recorded in the same way.

b.—The preservation of this specimen is distinctly unlike that of any truly Tertiary specimens from the same region and like that of some Pleistocene specimens.

c.—In the enormous collections subsequently made, nothing at all like this animal has turned up in the Tertiary but there are now a number of specimens known to be from the Pleistocene (or possibly early post-Pleistocene) that are specifically indistinguishable from this.

Like the type of *Felis veronis*, this specimen is not very exactly determinable in itself but a general comparison of all the materials establishes the probability that it belongs to the same group as *F. veronis* and hence that it is one of the large Pleistocene North American jaguars. When Hay described *F. veronis* he said that *F. augustus* "differs in various ways from the Vero specimen," without saying in what ways and obviously depending on the supposed difference in age rather than on actual comparison. Such comparison is necessary now that the two are seen to be of approximately the same age.

P^4 is of almost precisely the same length in the two types, 33.1 mm. in the type of *"Felis augustus"* and 33.4 mm. in the type of *"Felis veronis,"* but the latter is wider, 18.7 mm. as opposed to 16.7 mm. In keeping with this lesser width, the protocone in the type of *"F. augustus"* is smaller and it is directed somewhat more anteriorly. The anteroexternal cuspule is slightly smaller. The anterior border is emarginate between the protocone and the parastyle.[1] These and greater distinctions occur between different individuals of a single race of living jaguars, and the two fossils are otherwise almost identical in size and structure. In our very homogeneous *milleri* series the observed range (for only eight specimens) of the length:width index for P^4 is 173–200. The difference in this respect between *"F. veronis,"* index of type 179, and *"F. augustus,"* index of type 198, is therefore not enough, in itself, to demonstrate or suggest even a local racial difference, still less to validate specific separation. Of course a difference in the average characters of groups, corresponding with local racial distinction, is not excluded, but the specimens now available show that the two are very closely related and do not permit any valid taxonomic distinction, so that there is little choice but to consider the two names as synonymous.

In the U.S. National Museum collection there are two uncatalogued specimens of P^4, both broken, of an essentially similar feline, collected at Melbourne, Florida, by J. W. Gidley. One is 29.6 mm. in length and the other, on which this dimension cannot be exactly measured, was about 33 mm. in length. Both have the anteroexternal cuspule vestigial or absent, thus tending to eliminate this apparent difference from *"F. augustus,"* and in one the protocone, although broken, evidently projected forward as in *"F. augustus."* The specimens are from the same bed as the type of *F. veronis* and from a nearby locality and they tend to support the synonymy of that name with *F. augustus*.

Freudenberg (1910) described a left ramus with P_4–M_1 of a "jaguar-like felid" from presumably Pleistocene deposits at Tequixquiac, Mexico. The specimen itself was lost before Freudenberg's study was published, but a photograph was preserved and reproduced by him. His remarks are not explicit, but seem to imply that he had handled the specimen before it was lost, although his measurements are given as from the photograph and so are subject to error. As Freudenberg said, the photograph shows a jaw completely jaguar-like, as far as it goes, except that the coronoid process is peculiarly hook-shaped. If this character is real, it is far more likely to be pathological or otherwise anomalous than to be a feature of taxonomic value.

If the measurements from the photograph are reliable, they indicate an M_1 about 24–25 mm. in length (Freudenberg says 25, the published photograph suggests a slightly smaller size), while P_4 is about $23\frac{1}{2}$–24 mm. in length (24 according to Freudenberg). The length ratio P_4:M_1 was therefore probably between .94 and 1.00, with approximately .96 as the most

[1] I tentatively follow Wood (1929) in the nomenclature of these cusps.

likely figure. Not entirely distinctive, these ratios yet strongly suggest a jaguar or *P. atrox* in distinction from the pumas (see Fig. 5). The indicated size is smaller than specimens surely referred to *P. atrox* or its probable synonym *imperialis*, and compares closely with the large (male?) specimens of *P. onca augusta*, such as that from Craighead Caverns. It is at about the maximum for living jaguars belonging to *P. onca palustris* and is, as far as I know, larger than any living Mexican or Central American jaguars.

In the same deposit there was found an upper jaw with I^3, C, and P^{3-4}. This is at about the minimum size for *P. atrox* ("*P. imperialis*") from California. Freudenberg concluded that it belonged to an animal of about the same size as that just discussed. I think that it belonged to a slightly but distinctly larger animal. P^4 of the animal represented by the mandible would be almost surely between 30 and 34 mm. in length, with 33 as the most probable figure. The Tequixquiac P^4 measures 35 mm. As an isolated occurrence, this slight difference would not suggest any taxonomic distinction, but it happens that 35 mm. is just within the well-established range of the California *P. atrox* while 33 is not and is exactly right for typical *P. onca augusta*, as shown in Fig. 6. These facts tend to support the possibility that the Tequixquiac lower jaw is a large extinct true jaguar while the upper jaw is a female *P. atrox*. At the same time two other possibilities are not excluded by these unsatisfactory data: (1) that both Tequixquiac specimens belong to a small Mexican race of *P. atrox*, or (2) that both belong to a very large extinct Mexican race of *P. onca*. Except in size, there is no reliable difference between *P. onca* and *P. atrox* in the parts represented by these specimens.

"*Felis*" *hyaenoides* Freudenberg, from the same deposit, is a sabertooth and not a feline.

One other specimen that requires comment is the fragmentary lower jaw from Port Kennedy, Pennsylvania, referred by Cope to *Felis inexpectata* (Cope, 1899, Pl. XXI, figs. 1a, 1b). This belonged to an animal considerably larger than the type of *F. inexpectata* and the two could be of one race only on the assumption that the lower jaw is a male of maximum size and the type a female of minimum size, not impossible but improbable. Recently Gidley and Gazin (1938) have described what probably is a large individual of *F. inexpectata*, and its lower jaw and teeth are smaller than and different from Cope's referred specimen (see Fig. 3). They noted the disproportion of the Port Kennedy lower jaw and the possibility that it represents a different species.

The Port Kennedy lower jaw includes only M_1, the posterior part of P_4, and the ramus below these teeth and is not adequate for absolute determination in this difficult group. It does, however, differ from any known pumas and does not visibly differ from recent jaguars or the group of fossil jaguars described here, so that there is some probability that it belongs to the latter group.

These various occurrences of jaws and teeth thus demonstrate that jaguars formerly ranged widely over eastern United States. Although the specimens differ considerably in size and proportions, they do not differ more than do some individuals belonging to a single subspecies of recent jaguars and they do not serve to demonstrate that more than one group is represented, although of course this might prove to be true were more adequate series from the various localities at hand. No specific differences from *Panthera onca* are definitely shown, and the specimens must be referred to that species. On the basis of the present materials no distinction from *P. onca palustris* can be conclusively demonstrated. It is, however, manifestly improbable that this subspecies centering around the Chaco should have occurred in eastern United States. Moreover the few North American fossils are in several respects near the limits for the recent subspecies so that an adequate series might show a significant difference in average characters, although no such difference is yet shown. It therefore seems justified and is surely convenient to recognize this group tentatively as a distinct subspecies. "*Felis augustus*" is the oldest name applied

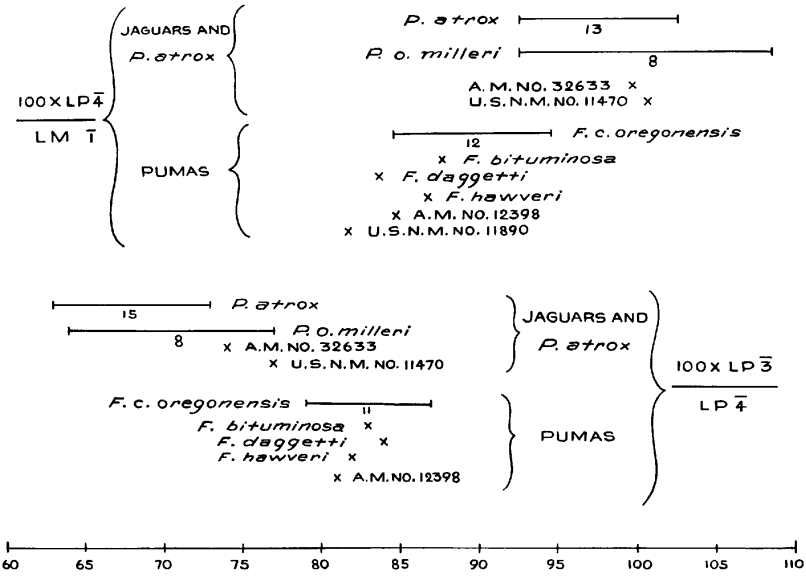

Fig. 5. Diagram of two dental indices in various large felines, as labeled. Crosses represent single specimens, lines samples of the size indicated by the number below the line. *P. atrox*, Rancho La Brea, data from Merriam and Stock. *P. o. milleri*, recent, Matto Grosso, specimens in American Museum. A.M. No. 32633, the Craighead Cat. U.S.N.M. No. 11470, Melbourne, Florida. *F. c. oregonensis*, living, western U. S., data from Merriam and Stock. *F. bituminosa*, type, data from Merriam and Stock. *F. daggetti*, type, data from Merriam and Stock. *F. hawveri*, type, data from Stock. A.M. No. 12398, Conard Fissure, Arkansas. U.S.N.M. No. 11890, Cumberland Cave, Maryland, data from Gidley and Gazin.

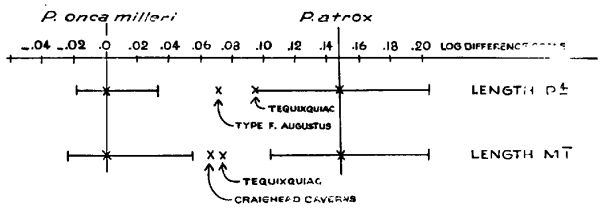

Fig. 6. Ratio diagram of lengths of P^4 and in various large felines, as labeled. Isolated crosses represent single specimens and lines represent larger samples with a cross at the mean value. *P. onca milleri*, Recent, Matto Grosso, specimens in American Museum. *P. atrox*, Rancho La Brea, data from Merriam and Stock. Tequixquiac, two specimens from that locality, in Mexico, data from Freudenberg. Craighead Caverns, the Craighead Cat.

to a probable member of this group, so that it may be provisionally designated as *Panthera onca augusta*.

The positive identification of *Panthera onca* adds another to the list of animals now mainly or typically South American but also typically North American in the Pleistocene. In view of the zoögeographic history of the two continents, it has long been assumed that the jaguar did migrate to South American from North America. It was therefore to be expected that it would occur in the North American Pleistocene and the establishment of this as a fact is welcome confirmation of the theory.

It is also interesting that the most northern and northeastern race now known, this extinct *P. onca augusta*, so closely resembles the most southern and southeastern living race, *P. o. palustris*. As far as now known, the former ranged in latitude from about 20° (if the Mexican specimen belongs here) or 28° (Florida) to about 43° north, while the latter is known from about 20° to 38°

south (fossil only in the southern part)—remarkable concordance. The jaguars between these extremes are all smaller in size. A similar tendency for the extreme northern and southern races to be largest is seen among pumas. In South America jaguars are also known fossil in higher latitudes than in North America, nearly to 52° south, and the form there found, *P. onca mesembrina* Cabrera, 1934, is larger than the forms ranging through the thirties in either continent. Finally the ally known from the most extreme latitude, about 65° north, is *P. atrox*, largest of all. (Of course it also ranged into relatively low latitudes during the Glacial Epoch.)

The accompanying diagrams (Figs. 4–6) show some of the important relationships of size and proportion in the North American fossil jaguars here discussed, as well as in the fossil pumas to be mentioned in more detail on later pages. Perhaps the most interesting feature of the largely self-explanatory diagrams is their demonstration (Fig. 5) that the index 100× length P_3/length P_4, although it does not distinguish *P. atrox* from *P. onca*, does in most and perhaps in all cases distinguish these two from any of the fossil and living pumas. It is more distinctive than the index 100× length P_4/length M_1, which has previously

LOWER JAWS

	P. onca augusta (fossil) Amer. Mus. No. 32633 (male?)	*P. onca augusta* (fossil) U. S. Nat. Mus. No. 11470 (female?)	*P. onca milleri* (recent) Observed range in eight specimens (including both males and females)
Length of ramus	203	ca. 173	162–206
Length of anterior border of symphysis	68	. . .	51–69
Depth below anterior end of P_4	42	ca. 34	33–40
Depth immediately posterior to M_1	43	37	35–41
Thickness posterior to M_1	17.5	16.0	13.5–18.5
C–M_1, inclusive	105.4	95.0	87.1–102.1
P_3–M_1, inclusive	65.7	56.5	54.1–59.7
Canine alveolus, length	ca. 26	ca. 20	19–26
Canine alveolus, width	ca. 22	ca. 18	16–21
P_3, length	18.2	16.1	14.0–17.3
P_3, width	9.0	8.3	7.4–9.5
P_4, length	24.7	21.0	19.8–22.9
P_4, width	12.4	ca. 11	9.8–12.8
M_1, length	24.6	20.7	20.0–24.0
M_1, width	12.7	11.1	10.2–13.0

UPPER JAWS

	P. onca augusta (fossil) Am. Mus. No. 32635 (male?)	*P. onca milleri* (recent) Observed range in eight specimens (both male and female)
I^1, maximum anteroposterior dimension of crown	6.9	5.9–6.9
I^2, same	8.0	6.6–7.9
I^3, same	11.0	8.8–11.2
Canine alveolus, length	21.8	20.1–26.2 (minimum for known males: 21.7)
Canine alveolus, width	16.9	15.4–18.6 (minimum for known males: 16.4)
Diastema, C–P^3, exclusive	13.7	10.0–17.5 (minimum for known males: 11.3)
P^2, length	8.5	6.8–7.7
P^2, width	5.8	5.2–5.8
P^3, length	19.6	18.2–21.2
P^3, width	10.1	9.1–11.4
Oblique distance, prosthion to lowest point on orbital rim[1]	102	85–110

[1] This odd and otherwise rather useless dimension is taken to give a rough idea of comparative gross size because it is one of the longest readily definable bone dimensions that can be taken on the fossil.

been used for this purpose and which does tend to distinguish jaguars and pumas but shows considerable overlap for values of the index from 93 to 95, inclusive.

The preceding measurements give a more complete roster of the dimensions of the better specimens of North American fossil jaguars and a comparison of them with a series of recent jaguars of one subspecies (or lesser local race).

NORTH AMERICAN FOSSIL PUMAS

Unlike jaguars, it has long been recognized that pumas occur in the Pleistocene of North America. I do not now have any important undescribed specimens of this group and the purpose of the present section is to point out that certain species or supposed species not generally recognized as such are pumas and to suggest some possible relationships and identities within the group.

Teeth of approximately puma-size found in the Pleistocene of the eastern states have usually been referred to or compared with *Felis inexpectata*, founded by Cope on an imperfect P^4 from Port Kennedy, Pennsylvania. In his definitive description (1899) Cope referred the species to *Uncia*, a genus used by him essentially as *Panthera* is in this paper and by most recent authors, but including the pumas as well as the lions, tigers, leopards, and jaguars. Cope then referred to "*Uncia inexpectata*" a lower jaw and various isolated teeth and skeletal parts. From his statements that *inexpectata* is a "large species of *Uncia*," the smaller skeletal parts "equal the average size of a jaguar," the species as a whole "as large as the jaguar," etc., he apparently based his final views more on these referred specimens than on the type, which is decidedly below average size for a jaguar and smaller than any but small females of the smallest races of jaguar, while it is of normal size for a robust puma. I have suggested above that his referred lower jaw probably does not belong to *F. inexpectata* and may well be a jaguar. This is probably true also of some of the referred skeletal parts, which I have not had occasion or opportunity to examine and restudy.

From the type alone it is almost impossible to determine the affinities of *F. inexpectata* beyond the fact that it is an advanced feline about as large as an average male of one of the larger living races of pumas, e.g., *F. concolor hippolestes* or *oregonensis*. As far as I know, the only previously referred specimens permitting close determination of affinities are those described by Gidley and Gazin (1938) from Cumberland Cave, Maryland, including P^4 and a lower jaw with P_4 and M_1. P^4 is larger than the type of *F. inexpectata*, but the size is within the probable range even for a local race and the characters are otherwise closely similar. The lower jaw is, as Gidley and Gazin remarked, definitely puma-like and not jaguar-like, although slightly larger than most or any recent pumas. The relatively shallow jaw, the definition of the anterior end of the masseteric fossa and its position distinctly posterior to M_1, and, especially, the small size of P_4 relative to M_1 strongly suggest the pumas and practically exclude close relationship to the jaguars. These specimens are from near the type locality of *F. inexpectata* (about 175 miles) and occurred in similar geological circumstances. Subject to the reservations imposed by the fragmentary and scanty material, they strongly suggest that the name *F. inexpectata* belongs to a puma and that most of the specimens so identified are pumas.

Smilodontopsis mooreheadi Hay, 1920, was based on another isolated P^4 found in the same region, at Cavetown, Maryland, under similar circumstances, and as far as such a specimen can be identified it appears to be the same as *F. inexpectata*.

It was apparently the belief that this tooth had no protocone that led Hay to consider it a sabertooth rather than a feline, with the additional evidence of the presence of a "preanterior lobe" (prostyle of Merriam and Stock). At the least, however, there is a protocone swelling and this and the (broken) third root were in the fe-

line position, quite different from the machairodontine. The preanterior lobe or prostyle is not a distinct cusp, as it almost always is in machairodontines, but only a slight rudiment such as is frequently present in felines. Moreover the protocone region shows distinct abrasion, probably post-mortem in origin, and it is possible and probable that a definite feline protocone was present before this occurred.[1] In short, this is a feline and not a machairodontine tooth.

Hay noted a resemblance to the type of *Felis inexpectata*, but said that the latter had a protocone and that on it the angle descending to the protocone from the outer cusp was stronger. The former distinction is now seen to be nonexistent or unreliable and the latter is slight and has no taxonomic value in allied recent forms. Hay's specimen is slightly larger, being 26.9 mm. in length (or 26.5, according to Hay), while Cope gives 24 mm. for his type, but this again is not sufficiently pronounced in itself to distinguish subspecies and still less species.

The synonymy is further supported by comparison with U.S. Nat. Mus. No. 11890, the P^4 from Cumberland Cave referred to *F. inexpectata* by Gidley and Gazin. This specimen is almost as large as the type of "*Smilodontopsis mooreheadi*," 26.5 mm. in length (26.6 according to Gidley and Gazin), and in general it is almost exactly like Hay's type except for the difference in preservation, not in original structure, of the protocone.

Felis longicrus Brown, 1908, is another supposed species not definitely distinguished from *F. inexpectata* by the known specimens and representing a species or subspecies of puma. It was based on an isolated P^4* from the Conard Fissure, Arkansas, with an isolated P_4** and several skeletal parts referred. The latter will be mentioned on a later page. As regards the type tooth Brown noted the close resemblance to *F. inexpectata* and at first referred this material to that species, but he later erected a new species because P^4 is more massive, the protocone larger and farther forward, the tooth narrower, the "paracone" (parametacone of Wood) larger, the "metacone" (metastyle of Wood) projecting farther backward and at a more obtuse angle. As between the two type specimens, these distinctions are all real, but comparison of a series of recent pumas and of several fossils found since Brown made his study shows that none of them is outside the probable variation of a single species or perhaps subspecies. The local races could well be distinct, but the isolated specimens in hand do not and cannot prove this. The following measurements show something of the normal range of variation in this and allied forms.

	"F. longicrus" type	*F. inexpectata* type. After Cope	*"Smilodontopsis mooreheadi"* type	U.S.N.M. No. 11890. After Gidley and Gazin	25 specimens of *F. concolor oregonensis*
Length P^4	27.3	24	26.9	26.6	20.2–25.3
Width P^4	13.4	(broken)	(abraded)	12.2	10.7–13.2

In the same publication Brown described a mandibular ramus that he referred questionably to *Felis cougar* (i.e., *Felis concolor couguar*). The specimen, Amer. Mus. No. 12398, was found with the type of *F. longicrus* (although clearly a different individual) and includes the canine and P_3–M_1. It certainly belongs to a puma of some sort and can be closely matched among modern pumas except that it is slightly larger than any individual with which I have compared it, without beings quite beyond the probable range for living forms. The small canine, high cheek-tooth crowns, shallow ramus, and particularly the length ratios of P_3:P_4 and P_4:M_1 are characteristically puma-like (see Fig. 5). M_1 in this jaw is 20.0 mm. in length. In twelve recent specimens of *F.*

[1] Drs. Gazin and Colbert also examined the specimen and agree with this statement.

* Misprinted M^1 in the original description.

** Misprinted P^3 and P_3 in different places in the original description.

concolor oregonensis, the index $100 \times LM_1 : P^4$ varies from 73 to 85 and averages 78.4. P^4 of this individual would thus probably be about 25.5 mm. in length and may have been anything from 24 to 27 mm. Thus, even without allowing for the undoubtedly considerable individual variation, this lower jaw could belong to an individual of about the size either of the type of *F. longicrus* or that of *F. inexpectata*. It is certainly most improbable that two distinct puma-like felids of so nearly the same size occurred together in Arkansas, and it seems almost certain that this is the lower jaw of "*F. longicrus*."

This specimen compares very closely with the lower jaw referred by Gidley and Gazin to *F. inexpectata*, both in form and, as the following measurements show, in size:

		Amer. Mus. No. 12398	U.S. Nat. Mus. 11890. After Gidley and Gazin
P_3	length	13.7	..
	width	7.0	..
P_4	length	17.1	17.2
	width	8.9	9.1
M_1	length	20.0	20.9
	width	9.2	9.6

These comparisons tend strongly to support the propositions (a) that *F. longicrus* and *F. inexpectata* are synonymous and (b) that all these forms are pumas.

If all these eastern specimens do belong to the same group, it was one that ranged and doubtless also averaged larger than do the living pumas, but one that intergraded with the latter in size and in all other known characters. Our knowledge is hardly yet adequate to demonstrate either the presence or the absence of specific distinction within the general fossil puma group. For convenience the specific name may be very tentatively retained, preferably in the form *Felis* (*Puma*) *inexpectata*, although the supposed species has not really been defined except for the very inadequate distinction that it probably attained a larger size than do recent specimens of *F.* (*P.*) *concolor*.

Various remains of fossil pumas, some of them relatively complete and excellently preserved, have been found near the Pacific coast. These have received three specific names, *Felis daggetti* Merriam, 1918, *Felis hawveri* Stock, 1918, and *Felis bituminosa* Merriam and Stock, 1932. I have not examined any original materials of these supposed species and can make no additions to the excellent descriptions given by Merriam and Stock, singly and together, and cannot make a revision of the somewhat less satisfactory taxonomy. It must be noted, however, that the published data do not compare *F. hawveri* and *F. bituminosa* and do not seem to demonstrate any valid taxonomic distinction between them, and that no comparison has been made with any of the eastern specimens of *F. longicrus*, *F. inexpectata*, etc., which, as far as they go are very similar to these western materials and could well represent races of the same species. It would also be advisable to consider the possibility that *F. bituminosa* (= *F. hawveri*?) is merely the female of *F. daggetti*, a possibility that seems to be rather supported than opposed by the published data. In any case, as Merriam and Stock have shown, these forms are true pumas and they may be referred to *Felis* (*Puma*), either as distinct species or as subspecies of the closely allied recent *F.* (*P.*) *concolor*.

PANTHERA ATROX

This species has been so fully described and compared and beautifully illustrated by Merriam and Stock (1932) that no additions are possible or necessary. It is mentioned here in order to express the opinion, based mainly on their data and consistent with their views but not so definitely expressed by them, that it is distinctly closer to *P. onca* than to the lions and tigers of the Old World and that it could, indeed, be called an extinct giant jaguar.[1] Despite this affinity, Merriam and Stock have well shown the *P. atrox* is sharply distinct in size range and in some characters of shape and proportion from *P. onca* (see, for instance, Fig. 10), and I agree that it merits specific distinction. The clearest taxonomic expression of these views would perhaps be to recognize the subgenus *Panthera* (*Jaguarius*) and to place *P. atrox* in it.

Although the type of *P. atrox* is from Natchez, Mississippi, the species has not otherwise been identified with certainty from anywhere east of the Rocky Mountains. A few limb bones and doubtful fragments suggest that it may have ranged in eastern United States, but it is in any case a rare fossil in this region. Similarly the large jaguars here called *P. onca augusta* have not yet been well identified from west of Nebraska, although some very dubious limb fragments suggest its possible presence in the farther west and it may have occurred in Mexico.

NOTES ON LIMB BONES

The preceding studies are based mainly on jaws and dentitions. The study of skeletal parts is more difficult and less conclusive because they are poorly known except in *P. atrox*, because they are sometimes less characteristic, and because adequate series of comparable recent specimens are difficult to obtain and have not been available to me. Nevertheless scattered skeletal remains afford some distributional data, or at least hints, that are of interest and a few of them warrant mention.

Gidley and Gazin (1938) referred to "*Felis* near *atrox*" scapholunar, second metacarpal, calcaneum, astragalus, and third and fifth metatarsals from Cumberland Cave. These elements are said to be too big to belong to a (recent) jaguar or puma, although smaller than any homologous *P. atrox* bones from Rancho La Brea. These various elements are not wholly diagnostic as to affinities with living pumas, jaguars, and *P. atrox*, especially as they evidently belong to some group distinct from any of these. They appear to me, on the whole, at least as puma-like as like the other two groups mentioned. The third metatarsal is stouter than in living pumas, and hence is jaguar-like in this respect, but all the bones otherwise agree fairly well with puma except in size. Their proportions, not only of the bones singly but also in comparison with each other, supposing all to represent a single species, are distinctive but are more like those of a puma than of a jaguar or *P. atrox*.

This is shown by the accompanying ratio-diagram, Fig. 7, the construction and interpretation of which are easy to accomplish but the principle of which is somewhat difficult to explain in words and is discussed in the last pages of this paper. An essential point is that if measurements of one individual, or means for a species, are set up in a vertical line, then series of homologous measurements of other indi-

[1] The habit of calling the machairodonts or sabertooths "tigers" and *P. atrox* a "lion" in the vernacular is misleading, to the point of confusing scientific thought as well as misinforming the non-scientific, and it should be abandoned. To most Americans, both South and North American, the American "lion" is the puma and the American "tiger" is the jaguar. *P. atrox* is certainly nearer the American "tiger" than the American "lion." Many paleontologists and laymen tend to think of it as similar to the African lion, and the usual restorations are simply drawings of an African lion slightly modified in proportions. The known facts would equally well or better justify restoration as a jaguar of suitably modified proportions, which would produce a profoundly different picture and habit of thought about the animal. Of course the sabertooths were neither lions nor tigers, a fact so well known to paleontologists that calling them "tigers" is not confusing to the well-informed, although it certainly creates confusion among the non-scientific public.

viduals with similar proportions will also tend to fall into vertical lines, farther to the right or left in proportion as the animal is larger or smaller than that used as a standard of comparison. Here the Cumberland Cave specimens are treated as standard and their dimensions set in a single vertical line. Then the more nearly another set of measurements comes to vertical arrangement, the more nearly its proportions approximate those of the Cumberland Cave material. None of the three comparisons gives close approach to a vertical, but the recent puma comes much nearer than do the jaguar or *P. atrox*, and hence shows

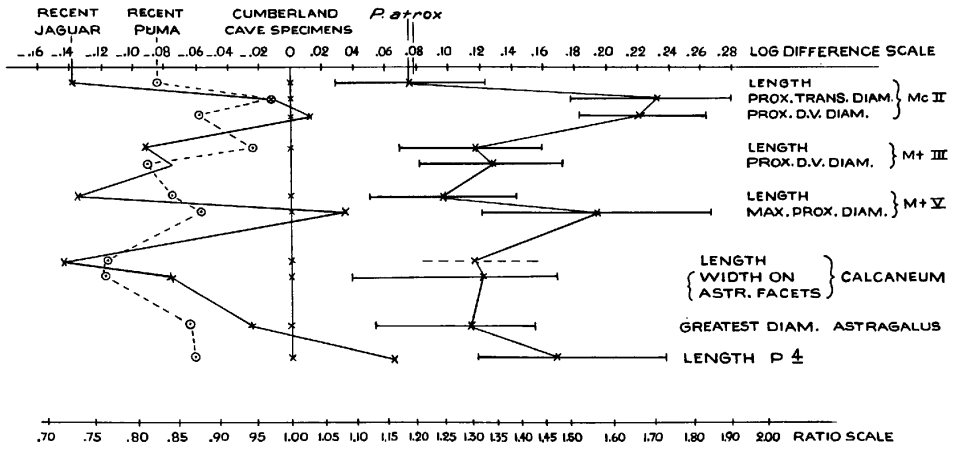

Fig. 7. Ratio diagram of dimensions of foot bones and P^4 in various large felines, as labeled. Recent jaguar and puma, from one individual of each, in American Museum. Cumberland Cave specimens, data from Gidley and Gazin. *P. atrox*, large samples from Rancho La Brea, data from Merriam and Stock; horizontal lines show observed range.

most nearly the proportions of the fossils. Closer approach would hardly be expected in view of the probability that the fossils are not all from one individual and are of a different species or subspecies from the living pumas. The diagram also shows that the fossils are closer to living jaguars and pumas than to *P. atrox* in size, and that they have about the same average proportions to a recent puma skeleton that the P^4 of *F. inexpectata* found in the same deposit has to P^4 of the same recent puma.

These bones do not belong to *P. atrox*, in which the range of variation is well established, and it is improbable that they belong to *P. onca*. On the whole they resemble the puma most and could well belong to a close ally of *F. concolor*, somewhat larger than the living members of the species. They are of about the right size to belong to *F. inexpectata* if, as is to be expected, that species was relatively small-headed, as is its ally *F. concolor*.

If these are skeletal elements of *F. inexpectata*, they tend to confirm the distinction of that species by showing that its feet may have had slightly different proportions than in *F. concolor*. The most definite suggestions are that the third metatarsal (at least) was relatively shorter and stouter in the extinct form and that the second metacarpal (at least) had a relatively narrower head.

In describing *F. longicrus*, Brown referred to it an ulna, complete except for the distal end, the distal end of a humerus, and various other isolated skeletal parts. The two principal specimens, figured by Brown on his Pl. XXIII, seem to me to be correctly referred and to represent *F. longicrus*, which I believe to be the same as *F. inexpectata*. They are very like *F. concolor* and hardly differ except in being larger and somewhat more elongate. They differ more markedly from the jaguar or *P. atrox*. In comparison with recent pumas as to proportions, they are appropriate in size

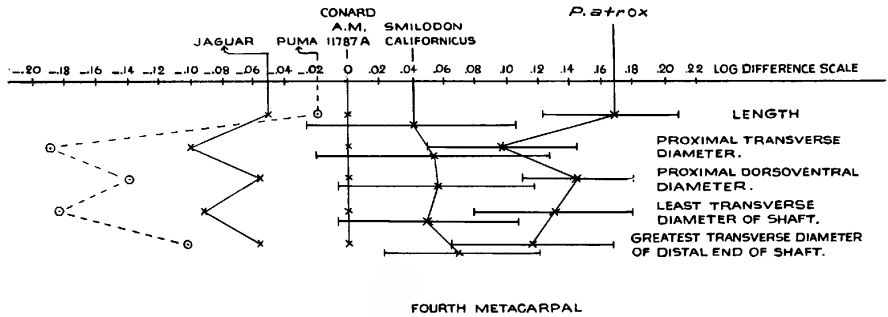

Fig. 8. Ratio diagram of dimensions of fourth metacarpal in various large felines, as labeled. Jaguar and puma, one specimen of each in American Museum. Conard, A.M. No. 11787A, one specimen from Conard Fissure, Arkansas. *Smilodon californicus* and *P. atrox*, large samples from Rancho La Brea, data from Merriam and Stock; horizontal lines show observed range.

for *F. inexpectata* (or *F. longicrus*), as Fig. 9B shows.

In the same collection, identified but not described by Brown as *F. longicrus*, there is a fourth metacarpal of considerable interest. Gidley and Gazin (1938, p. 53) mentioned it and noted resemblance to a saber-tooth.

The accompanying ratio diagram (Fig. 8) shows that the proportions are indeed more like *Smilodon* than like any of the large American true felines, notably in having the proximal and medial shaft transverse widths relatively greater than in the latter, including even the stout-footed jaguar and *P. atrox*. In fact, of the five standard dimensions all but the distal width are within the observed range of *Smilodon californicus* (on Merriam and Stock's data). Aside from these characters of size and proportion, however, there are marked structural differences between the species here in question, and structurally the Conard Fissure bone is quite unlike *Smilodon*,[1] as shown by the following table of some of these characters (again drawing on Merriam and Stock for data on *Smilodon* and *P. atrox*).

In these structural features *P. atrox*, *P. onca*, and the Conard metacarpal IV are

[1] In view of some previous misunderstandings regarding metrical methods, it may be well to emphasize that these ratio diagrams do not directly or adequately in themselves determine affinities. They show only what is put into them: the comparative proportions of the parts measured. Similarity of proportions is one of the important data for determining relationships, but it is not the only nor a sufficient datum.

Smilodon	*P. atrox*	*P. onca*	Conard Fissure Specimen	*F. concolor*
External border of unciform facet curved	Straight	As in *P. atrox*	As in *P. atrox* and *P. onca*	Nearly straight
Notch on internal border of proximal end obscure	Sharp and pronounced	Strong but less sharp	As in *P. onca*	Rather obscure
No dorsal indentation between unciform and MC III facets	Deep, narrow indentation	Shallow, broad indentation	As in *P. onca*	Shallow, narrow indentation
Unciform and MC III facets continuous but at a sharp angle	Continuous, almost same plane	As in *P. atrox*	As in *P. atrox* and *P. onca*	Roughly parallel, but MC III facet sharply offset distally relative to unciform facet
Usually two distinct facets for MC V, not reaching proximal margin dorsally	Facets usually continuous, reaching proximal margin dorsally	More as in *P. atrox*	Nearly like *P. atrox* or *P. onca*	Nearly like *P. atrox* and *P. onca*
Palmar end of distal keel pronounced, ending abruptly	Less prominent, ending less abruptly	About as in *P. atrox*	More as in *Smilodon*	About intermediate in character

slight variants of the same type, while *Smilodon* on one hand and *F. concolor* on the other are markedly different. Relationship of the Conard specimen with either of the latter two is improbable. Even in its *Smilodon*-like proportions it is definitely more like *P. onca* than like *F. concolor*, and on the whole its general structure is nearer to *P. onca* than to the very similar *P. atrox*. It is also nearer to *P. onca* in size and is roughly of the right size for a robust male of *P. onca augusta* (see Fig. 9A). It

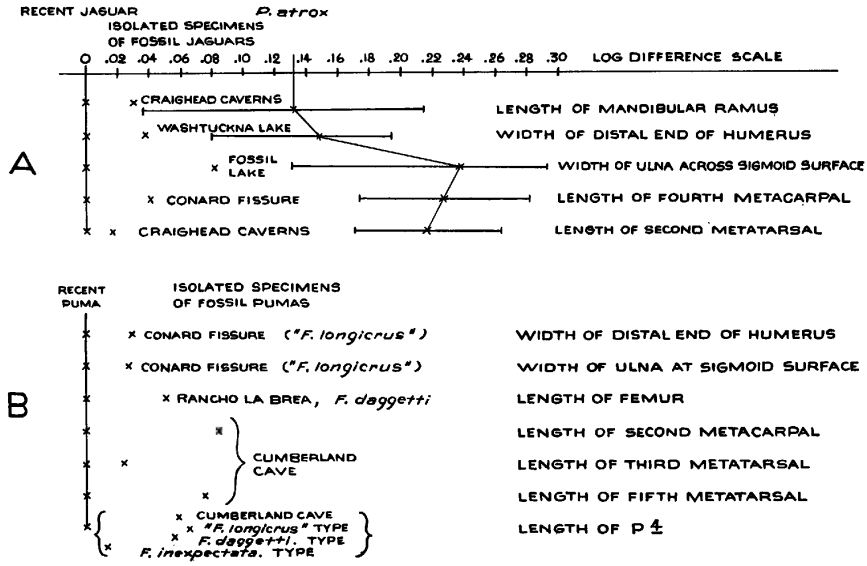

Fig. 9. Ratio diagrams of dimensions of various scattered large fossil feline remains, as labeled, compared with recent jaguar, A, and puma, B. Recent jaguar and puma, one specimen each in American Museum. *P. atrox*, sample from Rancho La Brea, after Merriam and Stock; horizontal lines show observed range. Isolated specimens from localities shown, further specified in text and in Figs. 4, 5, and 7.

may very well be a jaguar of this group, and it is very unlikely to belong to *F. longicrus* or *F. inexpectata*.

Hibbard (1939) has recently reported various feline remains from Meade County, Kansas. A left M_1 was classed as "*Felis* cf. *imperialis*" which according to Merriam and Stock (whose study apparently was not available to Hibbard) is indistinguishable from *P. atrox*. The tooth is said to measure 26 by 12.8 mm., hence is slightly smaller than the smallest Rancho La Brea specimens of *P. atrox*, for which Merriam and Stock give the minimum values 26.9 and 13. At the same time it is larger than any specimens now referred to *P. onca augusta*. The femur from Harvey Co. reported by Hibbard as *Felis* cf. *atrox* in the same paper has the same size relationships, being slightly smaller than Rancho La Brea *P. atrox* but larger than would be expected in *P. onca augusta* (in which this element is not known).

A fifth metacarpal from the same quarry as the "*Felis* cf. *imperialis*" tooth seems, as described and figured by Hibbard, to be within the probable range of *P. atrox* and somewhat enhances the probability that all these remains do belong to that species. A broken M_1 evidently belonging to a puma of normal size was found at the same place.

As far as they are known to me, none of the many discoveries in California suggests the presence there of large felines other than *P. atrox* and various pumas, but isolated discoveries in Washington and Oregon hint that a big true jaguar, like *P. onca augusta*, may possibly have occurred there. In the "Washtuckna Lake" collection from Whitman County, Washington, there is an

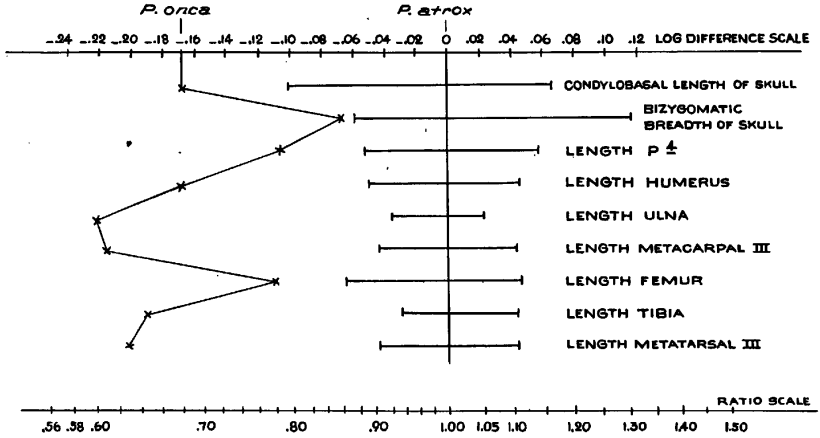

Fig. 10 Ratio diagram comparing various dimensions, as labeled, in a single recent jaguar and in the series of *P. atrox* described by Merriam and Stock.

imperfect distal end of a humerus, probably the basis for Matthew's report of "*Felix* cf. *imperialis*" (1902). It is very jaguar-like, as far as it goes, and on the basis of jaguar proportions belonged to an animal of about the size of the type of *P. onca augusta* (see Fig. 9A).

In redescribing the Fossil Lake, Oregon, material Elftman (1931) reported what he called "*Felis* sp. major" and "*Felis* sp. minor." The latter is smaller than the puma and so, although of great interest, is outside the scope of these notes. The former is known to me chiefly by Amer. Mus. No. 8680, the proximal half of an ulna. Morphologically this differs noticeably from the puma but is almost exactly like a recent jaguar except for its greater size. The same is true of this part in *P. atrox*, which the fossil also resembles except for smaller size. These relationships suggest *P. onca augusta* and the ulna may belong to or be allied with that group, although on the basis of jaguar proportions it is somewhat larger than would be expected for an animal as large as any definitely identified as one of these great true jaguars (see Fig. 9A).

CONSPECTUS OF LARGE PLEISTOCENE FELINES OF NORTH AMERICA

The following list includes most or all of the occurrences that have been published. The numbers correspond with those of the accompanying map (Fig. 11). Each entry includes the locality, principal reference (often but not always the first published notice), name used in that publication, nature of the material, and the present identification or comments.

1.—Port Kennedy, Pa. Cope, 1899: *Uncia inexpectata*, type P^4, referred jaw with P_4–M_1, various skeletal fragments. Type = *Felis* (*Puma*) *inexpectata*. Referred jaw perhaps *Panthera onca augusta*?

2.—Cavetown, Md. Hay, 1920: *Felis couguar*?, jaw fragment without teeth, and *Smilodontopsis mooreheadi*, type P^4. Both specimens probably belong to *Felis* (*Puma*) *inexpectata*.

3.—Cumberland Cave, Md. Gidley and Gazin, 1938: *Felis* cf. *inexpectata*, P_4 and lower jaw with P_4–M_1, and *Felis* near *atrox*, isolated foot bones. The teeth almost surely and the foot bones possibly belong to *F.* (*P*) *inexpectata*. The foot bones are not *P. atrox*.

4.—Craighead Caverns, Tenn. This paper: *Panthera onca augusta*, upper and lower jaws, etc.

5.—Vero, Fla. Hay, 1919: *F. veronis*, type P^4. Probably a synonym of *P. onca augusta*.

6.—Melbourne, Fla. This paper: *P. onca augusta*, lower jaw and various isolated teeth.

7.—Seminole Field, Fla. Simpson, 1929: *Felis* cf. *veronis*, several isolated teeth, and *Felis* cf. *inexpectata*, isolated P^4. Probably *P. onca augusta* and *F.* (*P.*) *inexpectata*.

8.—Sparta, Ill. Leidy, 1888: *Felis concolor*, cranium. Specimen not illustrated or restudied. Possibly recent?

9.—Natchez, Miss. Leidy, 1853; Merriam

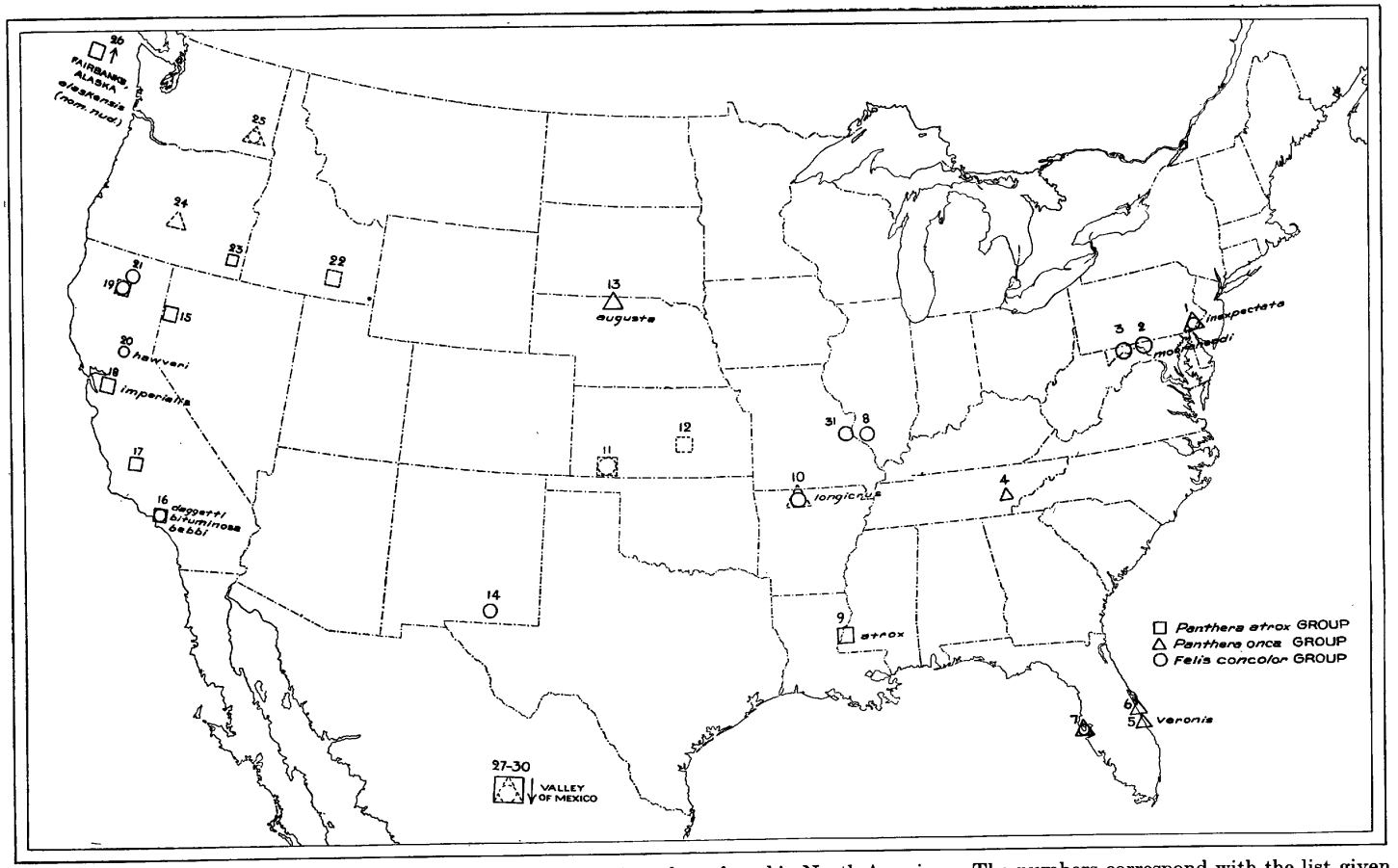

Fig. 11. Map showing places where large Pleistocene felines have been found in North America. The numbers correspond with the list given in the text. Trivial names of proposed species or subspecies are shown at their type localities. Symbols with broken outlines represent the more dubious identifications.

and Stock, 1932: *Felis atrox*, type, mandible with broken canine and P_3–M_1. *Panthera (Jaguarius) atrox.*

10.—Conard Fissure, Ark. Brown, 1908: *Felis longicrus*, type P^4, referred P_4 and limb fragments, and *Felis cougar* (?), mandible with C–M_1 and end of humerus. Teeth and most limb material probably *Felis (Puma) inexpectata.* One or two limb bones may be *P. onca augusta.*

11.—Meade Co., Kansas. Hibbard, 1939: *Felis* cf. *imperialis*, M_1 and fifth metacarpal, and *Felis* cf. *oregonensis*, broken M_1. The big cat may be *P. atrox*, although somewhat aberrant. The smaller is apparently a puma, but exact attribution uncertain.

12.—Harvey Co., Kansas. Hibbard, 1939. *Felis* cf. *atrox*, femur. Small for *P. atrox* but perhaps that species.

13.—Niobrara River, Neb. Leidy, 1873: *Felis augustus*, type, jaw fragment with P^4, humerus fragment. *Panthera onca augusta*, Pleistocene, not Miocene as hitherto reported.

14.—Burnet Cave, N. M. Schultz and Howard: 1935. *Felis concolor hippolestes*, limb fragments. A large puma, but materials perhaps inadequate for subspecific identification. Possibly post-Pleistocene.

15.—Astor Pass, Nev. Merriam, 1915: *Felis atrox*, P^4.

16.—Rancho La Brea, Calif. Merriam and Stock, 1932: *Felis atrox* (including *F. a. bebbi*, type, and *F. imperialis*), all parts of skull and skeleton, *F. daggetti*, type lower jaw, additional jaws and limb bones, *F. bituminosa*, type skull and jaws, additional skull, jaws, limb bones, *F. concolor*?, jaws. See discussion on previous pages.

17. –McKittrick, Calif. J. R. Schultz, 1938: *Felis atrox*, skulls, jaws, limb bones, *Felis daggetti*, skull.

18.—Livermore Valley, Calif. Leidy, 1873; Merriam and Stock, 1932: *Felis imperialis*, type upper jaw with P^3. Female or small individual of *P. atrox.*

19.—Potter Creek Cave, Calif. Sinclair, 1904; Bovard, 1907; Merriam and Stock, 1932: *Felis* sp., *atrox* group, upper milk carnassial, *Felis* sp. near *daggetti*, jaws, *F. hippolestes*, skull, partial jaws. The situation regarding the pumas is not clear to me from the published data and a single variety of *F. concolor* or of *F. daggetti* (if that is valid) may be present.

20.—Hawver Cave, Calif. Stock, 1918; Merriam and Stock, 1932: *Felis hawveri*, type lower jaw with P_3 M_1, *Felis* sp. near *daggetti*, partial skull, jaws, foot bones. The published data do not fully establish the presence of more than one species of puma, see above.

21.—Samwell Cave, Calif. Furlong, 1906; Stock, 1918; Merriam and Stock, 1932: *Felis* sp., *hippolestes* or near *daggetti*, skull. The specimen does not appear to have been fully described or exactly identified.

22.—American Falls, Idaho. Gazin, 1935: *Felis* near *atrox*, metacarpal and radius. Somewhat small for *P. atrox*, affinities very uncertain.

23.—Malheur Co., Oregon. Merriam and Stock, 1932: *Felis* cf. *atrox*, fragment of lower jaw without teeth.

24.—Fossil Lake, Oregon. Elftman, 1931: *Felis* sp. major, skeletal fragments. In part suggestive of a large jaguar, or perhaps small *P. atrox*, but exact identification very uncertain.

25.—Whitman Co. (near Washtuckna Lake), Wash. Matthew, 1902: *F.* cf. *imperialis*, distal end of humerus, *Felis* cf. *concolor*, limb fragments. The large cat may be a true jaguar, cf. *P. onca augusta*, but identification uncertain.

26.—Fairbanks, Alaska. Frick, 1930: *Felis atrox alaskensis*, type. Not described.

27.—Tequixquiac, Mexico. Freudenberg, 1910: *Felis imperialis*, skull fragment with I^3, C, P^{3-4}, *Felis* cf. *imperialis*, mandible with P_4–M_1, *Felis atrox*, upper jaw fragment without teeth. The first and third specimens probably represent *Panthera atrox*, and the second is perhaps a jaguar, see above.[1]

28.—San Luis, Mexico. Freudenberg, 1910: *Felis onca*?, broken canine. Very dubious, perhaps a jaguar.

29.—Mexico, exact locality unknown. Freudenberg, 1910: *F. concolor*, mandible. The identification is by Villada. Freudenberg had not seen the specimen and it has not been figured or described, nor are its age and geologic occurrence known. The record has no scientific value at present.

30.—Grand Canal, Valley of Mexico. Osborn, 1905: "large true cat, puma-like," skull. This specimen has not been described or figured and the identification and age are too uncertain to have positive value.

31.—Herculaneum, Missouri. Olson, 1940: *Felis* cf. *concolor*, upper carnassial.

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[1] *Felis hyaenoides* Freudenberg, 1910, is usually cited as another large Pleistocene feline, but it is probaby machairodontine and not feline. Freudenberg apparently later recognized this probability because in other lists (e.g., 1922) he referred the species to *Smilodontopsis.* It is based on an upper jaw fragment without teeth and is hardly identifiable in any case.

TAXONOMIC SUMMARY

The evidence reviewed on preceding pages suggests the following provisional taxonomic arrangement of the forms discussed in this paper.

FELIDAE

Felinae

GENUS **PANTHERA**

SUBGENUS **JAGUARIUS**

Panthera (Jaguarius) atrox (Leidy)

Felis atrox Leidy, 1853. Type, Phila. Acad. Nat. Sci. No. 12546, left lower jaw with broken C and P_3–M_1, from presumably Pleistocene deposit at Natchez, Mississippi.

Felis imperialis Leidy, 1873. Type, upper jaw with P^3, from presumably Pleistocene gravel at Livermore Valley, California.

Felis atrox var. *bebbi* Merriam, 1909. Type, Univ. Calif. No. 14001, skull, from Pleistocene asphalt pit at Rancho La Brea, California. Varietal or subspecific distinction from typical *P. atrox* not demonstrated.

Felis atrox alaskensis Frick, 1930. *Nomen nudum.*

Panthera (Jaguarius) onca augusta (Leidy)

Felis augustus Leidy, 1872. Type, U.S. Nat. Mus. No. 125, upper jaw fragment with left P^4 and broken P^3, from "Loup Fork" (Pleistocene not Miocene) of the Niobrara River, Nebraska.

Felis veronis Hay, 1919. Type, U.S. Nat. Mus. No. 11411, isolated left P^4, from Melbourne Formation, Pleistocene, at Vero, Florida.

Felis centralis? Gidley, in Hay, 1927, not *Felis centralis* Mearns, 1901.

GENUS **FELIS**

SUBGENUS **PUMA**

Felis (Puma) inexpectata (Cope)

Croculta inexpectata Cope, 1895. Type, Phila. Acad. Nat. Sci. No. 52, isolated right P^4, from Pleistocene fissure filling at Port Kennedy, Pennsylvania.

Uncia inexpectata Cope, 1899.

Felis longicrus Brown, 1908. Type, Amer. Mus. No. 11787, isolated P^4, from Pleistocene fissure filling, Conard Fissure, Arkansas.

Felis cougar Brown, 1908, not *Felis couguar* Kerr, 1792.

Smilodontopsis mooreheadi Hay, 1920. Type, U.S. Nat. Mus. No. 9212, isolated right P^4, from Pleistocene fissure filling at Cavetown, Maryland.

This species is inadequately distinguished from *F. concolor.*

Felis (Puma) hawveri Stock

Felis hawveri Stock, 1918. Type, Univ. Calif. No. 10636, left lower jaw with P_3–M_1, from Pleistocene deposit in Hawver Cave, California.

This species is inadequately distinguished from *F. inexpectata.*

Felis (Puma) daggetti Merriam

Felis daggetti Merriam, 1918. Type, Univ. Calif. No. 21572, left lower jaw with C and P_3–M_1, from Pleistocene asphalt pit at Rancho La Brea, California.

This species is inadequately distinguished from *F. inexpectata* and may possibly be based on a robust male of the species to which the type of *F. hawveri* belongs.

Felis (Puma) bituminosa Merriam and Stock

Felis bituminosa Merriam and Stock, 1932. Type, Los Angeles Mus. No. X8628, essentially complete skull and jaws, from Pleistocene asphalt pit at Rancho La Brea, California.

This species is inadequately distinguished from *F. inexpectata* or *F. hawveri* and may possibly be based on a female of *F. daggetti.*

EXPLANATION OF RATIO DIAGRAMS

Figs. 3 and 6–10 of this paper are constructed on a principle that I have not seen used elsewhere and they require some explanation. The method is one that lends itself readily to several useful types of graphic analysis and comparison and may therefore find wide application. I have found it convenient as an aid in distinguishing species and determining affinities, in sorting collections of bones, and in various ways beyond those illustrated in this publication.

The basic purpose of the diagram is to represent each of a number of analogous observations by a single entry and to plot them in such a way that the horizontal distance between any two of them will represent the ratio of either one of those two to the other. A simple plotting of calculated ratios, as in Fig. 5, has various and valuable properties, but it does not have the basic property sought for these more generalized ratio diagrams. It shows the ratios of various observations to one fixed standard or between fixed single items in one series to similar single

items paired with these in a related series, but it cannot show ratios between any two observations among many.

Consideration of the desired properties shows that the scale used must be logarithmic and not arithmetic. For instance, given absolute values a = 1, b = 2, and c = 4, the distance plotted between a and b should be the same as between b and c, because a:b = b:c. This is true on logarithmic but not on arithmetic coördinates. Since it is desired to ignore absolute values and represent only ratios, the simplest approach is to plot the logarithms of ratios. The logarithm of a ratio is the difference between the logarithms of the two absolute measurements entering into the ratio. The easiest method, then, is to plot the differences between logarithms. By using these differences as they are, not converting them to antilogs, a step may be saved and also ordinary arithmetic graph paper may be used, since plotting logs on this gives the same result as plotting antilogs on logarithmic paper.

For calculation, the direct measurements are first converted to their logarithms, three decimal places generally sufficing. Some one observation is then taken as "standard," to represent zero difference in logarithms which corresponds with the ratio 1.00. Observations larger than this then fall to the right of it at distances determined by their ratios to it, and smaller observations similarly fall to the left. Although the differences are thus calculated from some one standard, the resulting diagram shows not only ratios to that standard but also ratios of any combinations of observations: once the diagram is made, the zero point, or ratio 1.00 point, may be placed anywhere and ratios of all other observations to that point will still be correctly represented.

The arithmetic involved is much simpler than calculating even one set of ratios, not to speak of all possible sets, in spite of the fact that the resulting diagram does represent all possible sets. For instance, all the arithmetical calculation for the top line of Fig. 7 is as follows:

VARIATE: length of second metacarpal

Specimen		Measurement in mm.	Log	Difference from log of standard of comparison
U.S.N.M. No. 12840		94	1.973	0 (This is the standard here used)
Recent jaguar		68.3	1.834	−.139
Recent puma		77.2	1.888	−.085
P. atrox from Rancho La Brea	maximum	124.4	2.095	+.122
	app. mean[1]	...	2.048	+.075
	minimum	100.4	2.002	+.029

These figures can then be plotted against the log difference scale as shown.

[1] Data are from Merriam and Stock who do not give the mean or the figures from which it could be calculated. The range mid-point of the logarithms is taken as a sufficiently close approximation to the logarithm of the mean.

A scale for reading ratios directly from the diagram can easily be constructed and one correct for the ratio figures in this paper is printed at the bottom of Figs. 7 and 10. By copying this on a separate slip of paper, a movable scale can be made and the diagrams have the property that if 1.00 on the ratio scale be set at any specimen (whether the standard or not), the values of the ratios of all other specimens (set on the same horizontal) to this one can at once be read on the scale.

All the ratio diagrams are here reproduced on the same scale, so that a scale traced from Figs. 7 and 10 is valid for all. In study it is convenient to adhere to a single scale as far as possible. On study sheets, using arithmetic graph paper ruled in millimeters, I have found scaling log difference .02 as 10 millimeters to be most convenient.

Points marked on a single horizontal line represent different values of one variate. In the diagrams in this paper they represent homologous dimensions of different specimens, but any series of values of one variate can be used. The further and perhaps greatest usefulness of the method lies in the arrangement and interpretation of diagrams in which several different variates are involved, each represented by one horizontal series and these series arranged one below the other. The horizontal single variate series are so placed that related points fall into a single vertical line. For instance, different measurements on one individual may be placed in a vertical line, as in Fig. 9, or mean values for a unified sample may be so placed, as in Fig. 10, or values for a group of specimens may be thus arranged in order to test the hypothesis that they represent one species and to see what comparable species they most nearly resemble in their ratios to each other, as in Fig. 7.

The diagrams so constructed have many different uses and properties, some of which will be mentioned and others of which will be seen as the method is used.

If a series of measurements involves the same ratios as the standard of comparison, or, dealing with two individual animals, if a second animal has the same proportions throughout the parts measured as has the animal with which it is being compared, then this series being compared will also fall into a straight vertical line, regard-

less of whether the two animals are of the same absolute size or not. The more nearly the comparative series approaches the proportions of the standard series, the nearer will the comparative series come to falling into a vertical line. Thus in Fig. 7 the series representing the puma, although not in a vertical line, is obviously nearer to being in such a line than are those for the jaguar and for *P. atrox*. It therefore follows that the recent puma is, of these three, nearest to the proportions shown by the Cumberland Cave specimens.

If, as is generally the case, it can be postulated that scattered and isolated specimens belonged to animals with about the same proportions as some available standard of comparison, then the method makes it possible to compare the sizes of two or more animals known only by different specimens that are not homologous and that cannot be directed compared. Thus in Fig. 9 it is a permissible postulate that the fossil jaguars had approximately the proportions of a recent jaguar. The mandible and the metatarsal from Craighead Caverns, the humerus fragment from Washtuckna Lake, and the metacarpal from Conard Fissure fall in the diagram near a single vertical line. They therefore are shown to have belonged to animals of almost the same size. The ulna from Fossil Lake belonged, on this postulate, to a larger animal, but the probable amount of variation (as shown, for instance, by the comparable series for *P. atrox*) is such that it still is of a size probable for members of the same species.

A related use of the method is to estimate the relative sizes of missing parts of specimens, a procedure illustrated in Fig. 6. In this diagram the vertical alignment is on the means for *P. onca milleri*. The fact that the means for *P. atrox* also are almost precisely on a vertical line shows that in that species the average ratio of length P_4 to length M_1 was the same as in *P. onca milleri*. By plotting other specimens either of P^4 or of M_1, the most probable relative size of missing carnassials of the same animals is shown by a position on a vertical line through the point indicating a known carnassial. Thus P^4 is unknown in the Craighead Caverns cat, but erecting a vertical from the point representing its M_1 to the horizontal line on which P^4 is graphed shows that P^4 in this individual must have been smaller than in *P. atrox*, larger than in *P. onca milleri*, and almost exactly the size of the type of "*F. augustus*."

Similarly the unknown P^4 of the individual represented by the lower jaw from Tequixquiac (Freudenberg, 1910) was smaller than the P^4 known from the same locality and was almost exactly the size of the type of "F. *augustus*." Or, working in the opposite direction, the diagram shows that the missing M_1 of the type specimen of "*F. augustus*" was larger than in *P. onca milleri*, smaller than in *P. atrox*, and almost exactly as long as the lower carnassials known from Craighead Caverns and from Tequixquiac.

Finally when the sets of measurements used represent individuals or species that do, in fact, have different proportions, such diagrams show in a simple and immediately apparent way what these differences are. Thus Fig. 10 compares means and observed ranges for some of the most important dimensions in *P. atrox* with the same dimensions in one specimen of recent *P. onca*. The comparison would, of course, have been more reliable if averages for a series of *P. onca* were used, but for the limbs no such series is available to me and the individual comparison suffices for present purposes. From this diagram it is at once obvious that the recent jaguar has the skull broader relative to its length than in *P. atrox*, the distal limb segments shorter relative to humerus and femur, hind-limb longer relative to fore-limb but metatarsals about the same relative to metacarpals, carnassial about the same relative to gross size of skull, being larger relative to skull length and shorter relative to skull breadth, and so on. The proportions of any two of these variates in *P. onca* as compared with *P. atrox* can be directly observed in the chart without further work. To make similar comparison by non-graphic means would involve the arithmetic determination, for this example, of at least 108 different ratios, and when this labor was completed the results still would not be as clear and usable as they are in this one simple diagram.

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